THE LEAVES OF PODOPHYLLUM

J. ARTHUR HARRIS

An inspection of the leaves of the flowering stem of *Podophyllum peltatum* shows that they are not exactly the same size. Furthermore, the larger one seems generally to be inserted a little lower on the axis than the other of the pair. HOLM (**3**) found that the two leaves do not develop simultaneously but that one appears before the other. Concerning this point he writes:

> Of its two leaves, the one is developed earlier than the other. The base of the petiole of this leaf is dilated into a pair of broad wing-like stipules which envelop each other and enclose a small green leaf and a flower bud; thus the two green leaves did not develop at the same time, as it might seem when we examine the plant during its flowering period with its leaves apparently opposite.

Some of the teratological literature has an interesting bearing upon this question of the differentiation of the leaves. PORTER (**8**) illustrates one type in which the flowering stem bears two leaves, the peduncle apparently originating from one of the petioles two or more inches above their insertion. In another form there are three peltate leaves with the peduncle originating between the upper two, which are represented as about equal in size and opposite,[1] or some distance above the fork from one of the petioles. One of the leaves may be much reduced in size, or but one leaf—then apparently terminal and with the peduncle lateral—may appear. Finally both leaves may be absent. FOERSTE (**2**), apparently unacquainted with PORTER'S paper, redescribes these forms and adds other types, similar in a general way. The production of a small, not peltate lamina upon the peduncle is not very rare. The instance observed by BAILEY (**1**) of a flower replaced by a small erect leaf, and mentioned by PENZIG (**7**) as *sehr wunderlich*, was probably merely due to the early abortion of the flower bud in such a case.

The essential point to be gained from the foregoing observations is that the flowering stem of Podophyllum, instead of producing only two opposite leaves, may become an elongated shoot of at least three

[1] Here probably belongs the case described by TRIMBLE (**9**) which PENZIG (**7**) records as not clearly expressed.

leaves. In fact BRITTON and BROWN in the *Illustrated flora* describe the species as "bearing 1–3 similar leaves or sometimes leaflets." The third leaf is frequently small and not peltate, but it may be very similar to the others.

Knowing that more than two leaves are occasionally produced by the flowering stem, and that there appears to be a slight difference in the size and position of the two leaves in normal specimens, two questions occurred to me: (*a*) To what extent are the two leaves of Podophyllum really differentiated in type and variability? (*b*) What is the degree of similarity of leaves from the same individual?

A satisfactory measure of the area of a leaf so irregular as that of Podophyllum is obviously out of the question. It was necessary therefore to select some character other than size. The degree of lobing seems to be the only practicable one, although this character is not so definite as might be desired, and the determination is subject to considerable error due to personal judgment.

The margins of the very excentrically peltate leaves are irregularly toothed, lobed, or divided. It is quite impossible to draw a sharp line of distinction between the smaller lobes and the major divisions of the leaf, but I think that personal judgment would rarely vary greatly in the grading of an individual collection of plants. Perhaps less confidence is to be placed in a comparison of two or more lots taken at different times. In sorting the leaves into classes I counted as lobes the divisions extending at least half-way from the periphery of the leaf to the point of insertion on the petiole; divisions less sharply marked than this were not counted. Only normal plants—that is, those having only two leaves—were included in the collections. In sorting material to determine whether there is a differentiation between the upper and lower leaves of a pair, it is important that the appearance of the leaf lamina does not influence the judgment in any way. In dividing the nearly opposite leaves into upper and lower, the insertion of the petiole alone was examined. After the relative position of the two leaves was thus decided the counts were made.

The first lot of material examined was taken at Valley Park, near St. Louis, Mo., in May, 1906, when the plants were with partly grown fruit. In very few cases was there any question concerning the position to be assigned to the two leaves. All of the countings were made

by myself on one afternoon, so that I think there can be but little error due to variation of judgment. All plants were taken at random, and none were discarded except because of mutilation which rendered the countings untrustworthy, save three which had an extra lamina at the base of the peduncle. The data for the 400 flowering stalks counted appears in the form of a correlation table as table I.

TABLE I

UPPER LEAF

LOWER LEAF	4	5	6	7	8	Totals
5	1	4	3	..	..	8
6	4	34	66	1	..	105
7	1	52	144	28	..	225
8	..	2	22	16	..	40
9	..	..	6	10	1	17
10	..	1	1	2	1	5
Totals...	6	93	242	57	2	400

The second series I secured in the woods at Palos, Athens Co., Ohio, in early July, 1908. It was really too late in the season to work to advantage, for many of the plants were so badly dried that they had to be discarded. I see no reason for believing that this discarding of individuals too brittle to be counted introduces any element of error into the work, though it did considerably increase the labor. The countings were made in as nearly the same manner as for the first series as possible. The data are given in table II.

TABLE II

UPPER LEAF

LOWER LEAF	2	3	4	5	6	7	8	Totals
4	1	..	1	..	..	..	..	2
5	..	..	13	24	..	..	..	37
6	..	2	12	80	4	1	1	100
7	1	..	9	121	42	8	..	181
8	..	..	..	2	8	8	..	18
9	..	..	..	..	1	..	..	1
Totals..	2	2	35	227	55	17	1	339

The physical constants for these two lots are laid side by side in table III. To permit of easy comparison the differences between the constants for the two series, and the probable errors of the differences, are given. Comparing the means for both upper and lower

leaves for the two habitats, we notice that they differ by ten to twenty times the probable errors of their differences. The standard deviations differ by only one and a half to three times the probable errors of their differences. Perhaps the differences between the means of the collections from the two habitats are significant statistically, but I attach no biological importance to the differences, since they may be due merely to some slight local environmental condition. The variabilities certainly do not differ significantly.

TABLE III

VARIATION CONSTANTS FOR LOBING OF PODOPHYLLUM LEAVES

Series of material	Average and probable error	Standard deviation and probable error	Coefficient of variation
VALLEY PARK, MO.:			
Lower leaf	6.920± .029	.848± .022	12.25
Upper leaf	5.890± .022	.666± .016	11.30
Difference	+1.030± .036	+.182± .027	+ 0.95
PALOS, OHIO:			
Lower leaf	6.528± .029	.792± .021	12.13
Upper leaf	5.139± .027	.742± .029	14.43
Difference	+1.389± .040	+.050± .036	− 2.31
DIFFERENCES:			
Lower leaf	+0.392± .041	+.056± .030	+ 0.12
Upper leaf	+0.751± .035	−.076+ .025	− 3.13

Taking now the question (*a*), that of a differentiation between the upper and lower leaves, we note that the means differ in both cases by about thirty times the probable error of their differences, and that the lower leaf has in both cases about one lobe more than the upper. The standard deviations differ by an amount which can hardly be regarded as significant. The relative variability as measured by the coefficient of variation is in one case higher for the upper leaf and in one case lower. After calculating the constants for the first series of material, I thought that perhaps the variability of the more distally placed leaf would be regularly lower than that of the more proximal one, as PEARL (4) found the variability of the whorls in Ceratophyllum to be. But the second series does not support this idea.

It may be interesting to compare the variability in the lobing of the leaves of Podophyllum with that of other leaf characters given by PEARSON (5). From page 361 I note the following values of the coefficient of variation for leaf characters:

Holly, Dorsetshire, prickles on leaves	26.29
Holly, Somersetshire, prickles on leaves	18.74
Ash, Dorsetshire, leaflets on leaves	18.65
Ash, Monmouthshire, leaflets on leaves	18.57
Ceterach, Somersetshire, lobes on fronds	18.25
Wild ivy, mixed, leaf-indices	17.77
Spanish chestnut, mixed, veins in leaves	15.72
Ash, Buckinghamshire, leaflets on leaves	15.46
Spanish chestnut, Buckinghamshire, veins in leaves	14.31
Beech, Buckinghamshire, veins in leaves	10.77

It appears by these comparisons that the lobing of the leaves of Podophyllum is rather less variable than leaf characters in general.

Turning now to the question of the degree of similarity between the two leaves, and calculating the coefficient of correlation between the number of lobes on the lower leaf and the number of lobes on the upper leaf by the familiar product-moment method, we find the correlations,

For the Valley Park series	.428± .028
For the Palos series	.468± .029
Difference	.040± .040

I was considerably surprised when these values turned up on my dividing machine. A priori, I would have expected considerably higher coefficients, say about .700, for the correlation between organs so closely associated as the leaves of Podophyllum. In thinking of the correlation between the leaves of Podophyllum, it had always seemed to me organic rather than homotypic in nature. The two leaves seemed so nearly exactly opposite and the whole "normality" of the plant seemed to depend so much upon their forming a symmetrical pair that I had expected the usual homotypic resemblance plus something more.[2] But instead we find values which fall directly in line with those found by PEARSON and others for homotypes in general. Taking merely the leaf characters noted above, we find the homotypic relationship calculated by PEARSON and his coworkers (5) to be the following:

Ceterach, Somersetshire, lobes on fronds	.631
Holly, Dorsetshire, prickles on leaves	.599

[2] For a clear statement of the distinction between organic and homotypic correlation see page 340 of PEARSON'S splendid reply (6) to BATESON'S criticism of the theory of homotyposis.

Spanish chestnut, mixed, veins in leaves	.591
Beech, Buckinghamshire, veins in leaves	.570
Spanish chestnut, Buckinghamshire, veins in leaves	.466
Ash, Monmouthshire, leaflets on leaves	.405
Ash, Dorsetshire, leaflets on leaves	.396
Ash, Buckinghamshire, leaflets on leaves	.374
Holly, Somersetshire, prickles on leaves	.355
Wild ivy, mixed, leaf-indices	.273

Some of these are slightly higher and some slightly lower than our coefficients; but when the probable errors attached to all constants are borne in mind, I think we cannot assert that our values are very different from those obtained by English biometricians for other leaf characters. Furthermore PEARSON shows reasons for considering some of his values too high and some too low for true homotypic relationships. For instance, ceterach is said by botanists to be largely influenced by growth and environment.[3]

There still remains one possible reason for thinking that the real correlation between the number of lobes on the leaves of the same flowering stalk may be somewhat higher than is indicated by these constants. The May apple spreads considerably by rootstocks. My plants from both habitats were taken from quite a wide stretch of woods, but a considerable number of the plants are doubtless vegetatively related. I do not believe this has a very large influence in my series, but it is proper to mention the point.

3 From the arithmetical side there are also difficulties. I did not apply SHEPPARD'S correction for the second moment in calculating my standard deviations. Perhaps this should have been done, but until some mathematician works out the theory, biologists will not know what rule to follow in the case of integral variates. In the case of a range of variability so narrow as we have here, SHEPPARD'S correction would make a considerable difference, raising the coefficient of correlation by lowering the standard deviations. So perhaps our values should be a little higher.

There is also the question of leaves which fall on the borderline between n and $n+1$ lobes. In the present study I carefully tried to throw these into the class to which they most nearly belonged, just as one would have to do in the case of real integral variates. But after all, the lobing of the leaf of Podophyllum is not a case of discrete variation, and if I were repeating the work I would divide questionable cases between adjoining grades. Probably this would not make a very great difference in the end result.

The reader will note, too, that I am discussing "homotypic" correlation on series of material which I have just demonstrated to be differentiated. But I think I am quite justified in treating the material as I have done, for lower and upper leaves have always been kept separate. There has been no mixing of heterogeneous material.

Summarizing, we may say that so far as our materials show: (*a*) there is a sensible differentiation between the two leaves of the flowering stalk of Podophyllum in the number of lobes, but apparently not in the variability of the lobes, at least not in their relative variability; and (*b*) the correlation between the number of lobes on the two leaves of the stalk lies somewhere in the neighborhood of .45, agreeing well with the homotypic correlations for leaf characters in other species.

CARNEGIE INSTITUTION OF WASHINGTON

LITERATURE CITED

1. BAILEY, W. W., Bull. Torr. Bot. Club **13**:111. 1886.
2. FOERSTE, AUG., The May apple. Bull. Torr. Bot. Club **11**:62–64. 1884.
3. HOLM, T., *Podophyllum peltatum:* a morphological study. BOT. GAZETTE **27**:419–433. 1899.
4. PEARL, R., Variation and differentiation in Ceratophyllum. Pub. 58 Carnegie Inst. Wash. 1907.
5. PEARSON, K., and others. Mathematical contributions to the theory of evolution. IX. On the principle of homotyposis and its relation to heredity, to the variability of the individual, and to that of the race. Phil. Trans. Roy. Soc. Lond. A. **197**:285–379. 1901.
6. ———, On the fundamental conceptions of biology. Biometrika **1**:320–344. 1901.
7. PENZIG, O., Pflanzenteratologie. Genoa. 1890–94.
8. PORTER, T. C., Variation in *Podophyllum peltatum*. BOT. GAZETTE **2**:117, 118. 1877.
9. TRIMBLE, W., Teratological notes. Bull. Torr. Bot. Club **9**:10. 1882.